Soil Physical Environment and Root Growth in Northern Climates

Gurdarshan S. Brar and Charles M. Reynolds   May 1996

Abstract

Understanding the growth and function of plant roots in cold climates is critical, but examination of root systems to elucidate their link to production is expensive and labor-intensive. Limited information is available on the root growth and functions of plants grown in northern climates. Our objective is to present an overview of the influence of physical edaphic factors on plant root systems with special emphasis on models that are available for simulating root growth. This report summarizes the impact of the soil physical environment (soil water, soil temperature, soil air, physical impedance, and spatial variability) on root uptake and growth. Roots grow because new cells are formed in the meristematic tissue near the root tip, and these newly formed cells increase in volume, pushing the root tip forward if growth conditions are satisfactory. Rapid elongation of primary roots, combined with well-developed secondary roots, allows the plants to exploit moisture and nutrients from a greater soil volume. Root and shoots are strongly interdependent. The roots receive photosynthates and growth hormones from shoots and in return furnish water and nutrients to the shoots. Several root growth models have been developed during the past decade; however, none addresses the problems associated with cold regions. The models reported in the literature can be classified as 1) simple models, 2) carbon partition models, 3) growing degree day-based models, 4) soil parameter-based models, and 5) arctic plant growth models.

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PREFACE

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Soil Physical Environment and Root Growth in Northern Climates

GURDARSHAN S. BRAR AND CHARLES M. REYNOLDS

INTRODUCTION

Plant roots grow because new cells form in the meristematic tissues near the root tip and the newly formed tissues expand in volume, pushing the root tip forward. The amount of water and the nature of nutrient uptake from the root zone are established by the interactions of various physical, chemical, and biological processes. After many years of scientific discoveries, we understand how water and chemicals enter the soil and are transported through the root zone. However, our understanding of the fundamental aspects of growth and proliferation of plant roots within the cold soil environment is still incomplete, because of the vast complexity of the various interacting processes involved.

During the last decade, root research has received its strongest emphasis from plant physiologists, ecologists, and soil scientists. Limited information is available on water and nutrient uptake by roots in cold regions. Billings (1992) reported that in northern climates, plant metabolism, growth, and reproduction are controlled by the interactions of the soil physical environment and the genetic structure of cold-adapted flora. In these cold regions, the major constraints to root growth are the presence of continuous permafrost in the subsurface and the short growing season (Fig. 1). The literature provides information on the genetic structure of cold-tolerant plants; however, limited information is available on the root growth and development in northern climates. Therefore, this review focuses on the soil physical environment and its effect on root growth in cold climates.

The soil physical environment will be characterized by temperature, water, aeration, mechanical impedance, and spatial variability. The soil physical environment required for the development of an efficient root system must be free from stresses caused by mechanical, water, oxygen, and cold-temperature conditions. Soils, because they vary texturally, structurally, in porosity, and pore size distribution, differ greatly 1) in their resistance to root penetration, 2) how they collect, store, and release water for root uptake, and 3) how they maintain aeration by gas exchange with the atmosphere.

The objective of this report is to present an overview of plant root growth and development under soil physical environments with special emphasis on models that are available for root growth simulation. The physical edaphic factors, as they occur naturally or are created by human activities, and their effects on root growth are presented, beginning with brief background information on root origin and distribution, growth, development, and functions.

ROOT ORIGIN AND DISTRIBUTION

Seeds germinate and primary roots originate from the radicle. Roots also originate from stem nodes on stolons, bulbs, and rhizomes of grasses, or from the hypocotyl of certain dicotyledonous plants (dicots, Fig. 2). As dicots grow, the laterals of the first order emerge from the main root followed by laterals of second, third, fourth, and even fifth order (Barley 1970). In monocotyledonous plants (monocots, Fig. 2), the seminal (primary) roots originate from primordia in the embryo, and crown (nodal, adventitious, or brace) roots arise from foliar nodes of the growing plant (Russell 1977, Klepper 1991). The growth rate of
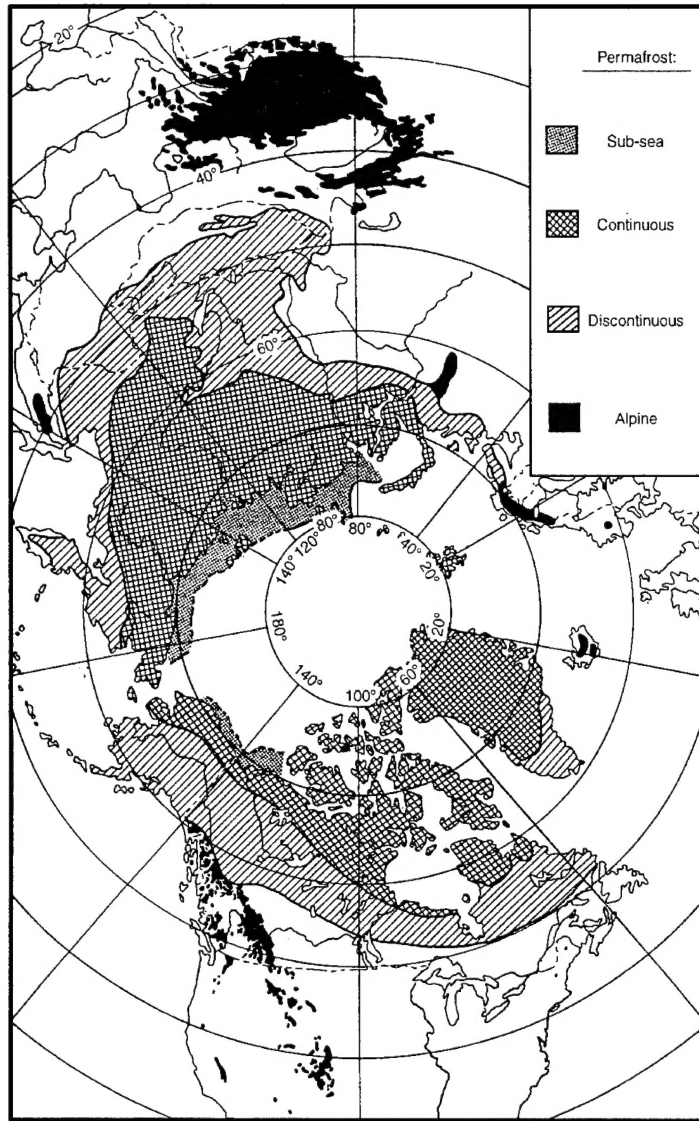
Figure 1. Distribution of permafrost in the Northern Hemisphere (after Péwé 1983).
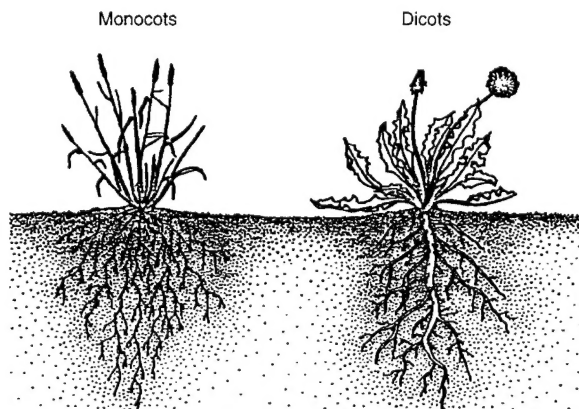
Figure 2. Gross morphology of two root types; a fibrous root system (left) and a tap root system (right) in soil (after Stem 1982).

the primary roots slows down after the initiation of nodal roots. When the formation of crown roots is delayed, the plants rely entirely on the seminal root system for acquisition of water and nutrients during the seedling establishment stage.

There is a continuous spectrum between the two extremes of fibrous and tap root systems (Rendig and Taylor 1989). Monocot plants have fibrous root systems, and dicots have some variant tap root system.

Monocots

Under favorable conditions, monocot root extension rates are rapid. During the vegetative phase of plant growth, root depth and root length density (m roots m^{-3} soil) increase with time.

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However, even during seed sink initiation, roots do not completely stop growing. Root length density generally decreases with increased soil profile depth.

Seminal and crown roots are different morphologically and functionally. For instance, in wheat and grasses, seminal roots go deeper, are thinner in size, and are more branched compared to crown roots (MacKey 1973). The crown root system is more flexible regarding development under changed environmental conditions (Tennant 1976).

Dicots

The diameter of dicot roots decreases with increase in order (Rendig and Taylor 1989). The average functioning life of higher-order roots may be 10 to 20 days. Higher-order roots form when the environmental conditions are favorable and die when water and nutrients are depleted in their immediate vicinity. When soil water potential decreases below –0.2 MPa for 7 to 10 days, about 80% of the roots can become senescent.

Time and environmental conditions substantially influence the initiation rates of new roots and death of old roots. Therefore, the root length density and root length per plant fluctuate during the season. As observed in monocots, the root growth of dicots continues during the reproductive phase.

ROOT GROWTH AND DEVELOPMENT

Roots grow because new cells are formed in the meristematic tissue near the root tip, and these newly formed cells increase in volume, pushing the root tip forward if growth conditions are satisfactory (Taylor and Brar 1991). Before the cell starts expanding, the water potential inside the cell, ψ^{inside}, is equal to the water potential outside, $\psi^{outside}$, and $\psi^{inside} = \psi_p + \psi_o$, where ψ_p is turgor potential and ψ_o is the osmotic potential. Processes responsible for cell expansion are described by Hsiao and Bradford (1983) as

1. Cell-wall loosening or relaxation, i.e., $\psi^{outside} > \psi^{inside}$;
2. Water flow into the cell, diluting its solutes;
3. Water influx causing the cell wall to expand until ψ^{inside} and $\psi^{outside}$ are nearly equal.

These processes occur simultaneously and continuously in the plant root system.

Rapid elongation of primary roots, combined with well-developed secondary roots, allows the plants to exploit moisture and nutrients from greater soil volume (Harris 1977). Main axis root elongation rates of forage legumes were significantly correlated with seed weight (Brar et al. 1990a). Cultivars within the species had significant impact on root elongation rates. Similarly, root growth also varied greatly among plant species (Stone and Taylor 1983, McMichael et al. 1985, Brar and Palazzo 1995). The rate of root elongation may range from 0.5 to 3 cm day^{-1} (May et al. 1965) or more (Taylor and Ratliff 1969). Elongation rates of main root axes, primary laterals, and secondary laterals of small grain cereals grown in a relatively favorable laboratory environment were 20, 0.5, and 0.1 cm/day, respectively (Lungley 1973). The root extension rates decreased with increased plant age and were negligible in perennial crops (Hillel and Talpaz 1976).

ROOT–SHOOT RELATIONSHIPS

Root and shoots are strongly interdependent. The roots receive photosynthates and growth hormones from shoots and in return furnish water and nutrients to shoots (Taylor and Arkin 1981). After seed germination, plants generally contribute the major portion of the metabolites towards root expansion. For instance, the radicle grows faster than the plumule of wheat after germination; however, the trend is reversed at later stages of growth. Root:shoot ratios differ depending on environmental conditions around the plant.

Relationships of root and shoot growth for 22 winter wheat crops grown in the United Kingdom are illustrated in Fig. 3. Dry matter is equally partitioned between roots and shoots in the early stages of wheat growth, but at anthesis the root-per-plant ratio has fallen to 0.1 (Barraclough et al. 1991). The total shoot dry matter of 18 t ha^{-1} was accompanied by a root dry matter of 1.5 t ha^{-1}. Winter crops with longer growing seasons produced more shoot dry matter compared with spring crops, and similar trends were observed for the root system. A well-developed root system was observed for winter wheat compared with arable crops (Table 1).

Soil physical factors such as temperature and soil water potential affected the root:shoot ratio of sorghum seedlings (Brar et al. 1992). The ratio significantly increased with increases in soil temperature from 15.9 to 25.2°C and declined at temperatures of 30.2 and 35.8°C (Table 2). Furthermore, the ratio was greater with –0.1 than –0.03
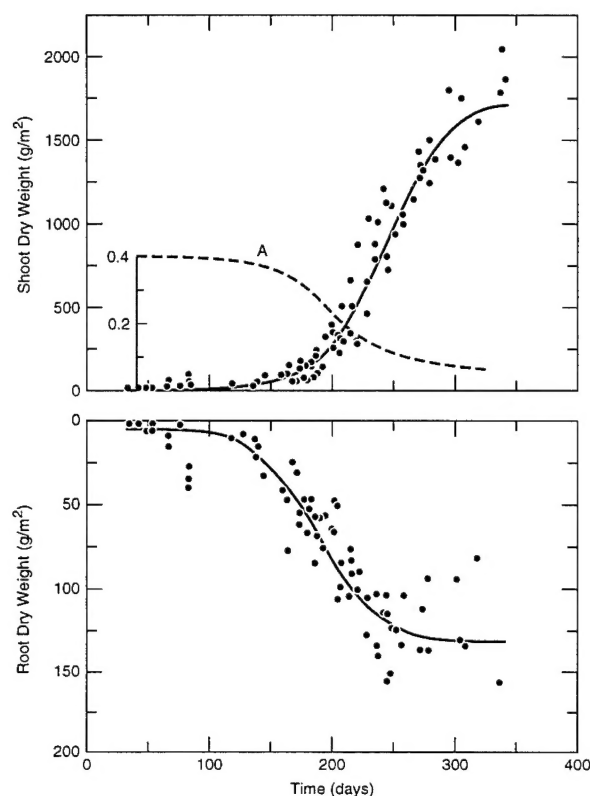
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Figure 3. The growth of roots and shoots of high-input UK winter wheat crops in relation to the number of days from sowing. A = anthesis (after Barraclough et al. 1991).

Table 1. Maximum root length density, MRLD, (cm cm^{-3}) in the topsoil for various field crops.

Crop	MRLD	Reference
Winter wheat	12.2	Barraclough et al. (1989)
Winter rape	9.7	Barraclough (1989)
Spring barley	4.2	Welbank et al. (1974)
Maize (US)	4.0	Mengel and Barber (1974)
Spring wheat	3.3	Welbank et al. (1974)
Sugar beet	2.6	Brown and Biscoe (1985)
Pea	2.5	Greenwood et al. (1982)
Potato (NL)	1.9	Vos and Groenwold (1986)
Soybeans (US)	1.0	Barber (1978)
Broad beans	0.8	Greenwood et al. (1982)

Table 2. Root:shoot ratio of sorghum seedlings as affected by soil temperature and soil water matric potential. Data are means of three observations (after Brar et al. 1992).

Soil temperature (°C)	Root:shoot ratio Soil water potential (MPa)	
	−0.03	−0.10
15.9	0.34[b]*	0.43[ab]
20.5	0.39[b]	0.60[a]
25.2	0.75[a]	0.66[a]
30.2	0.39[b]	0.44[ab]
35.8	0.36[b]	0.06
LSD ($P \leq 0.05$)	0.035	0.42

* Within columns, means not followed by common letter differ ($P \leq 0.05$) according to Fisher's Least Significant Difference Test.

MPa soil water potential at 15.9, 20.5, and 30.2°C. Significant correlations ($r^2 = 0.96$) were obtained for shoot dry matter with root dry matter of tall and fine fescues (Brar and Palazzo 1995). Furthermore, significantly greater root–shoot growth of tall fescue was observed in silt loam compared with sandy soil. Cool-season grasses (C$_3$ photosynthesis) had lower root:shoot ratios compared with warm-season grasses (C$_4$ photosynthesis).

During the last seven years, plant water relation concepts have changed, and roots rather than shoots are considered to regulate plant growth and development in drying soil. Kramer (1988) reported that 50 years of progress in our understanding of plant water relations were lost by shifting emphasis away from the soil to the shoots of the plant. Recent evidence suggests that root signals influence stomatal behavior, leaf initiation, leaf expansion, and other development processes (Davies and Zhang 1991). Current thinking in this area is summarized in Figure 4.

ROOT FUNCTIONS

The major functions of plant roots are water transport, nutrient uptake, plant anchoring, and plant metabolite storage. Roots absorb water and nutrients simultaneously from deep and shallow soil horizons and from moist and partially dry soil (Rendig and Taylor 1989). Plant anchoring is important for the shoot to emerge through crusted soils and for roots to force a path through a soil matrix to keep the plant from falling. Storage capacity of metabolites is greater for fleshy roots compared with grasses. Roots are believed to be the primary source for growth regulators such as cytokinin, gibberellin, abscisic acid, and ethylene.

Water uptake

Soil water uptake is usually assumed to be proportional to the product of the rooting activity, hydraulic conductivity, and potential energy terms for any specific soil volume element of uni-

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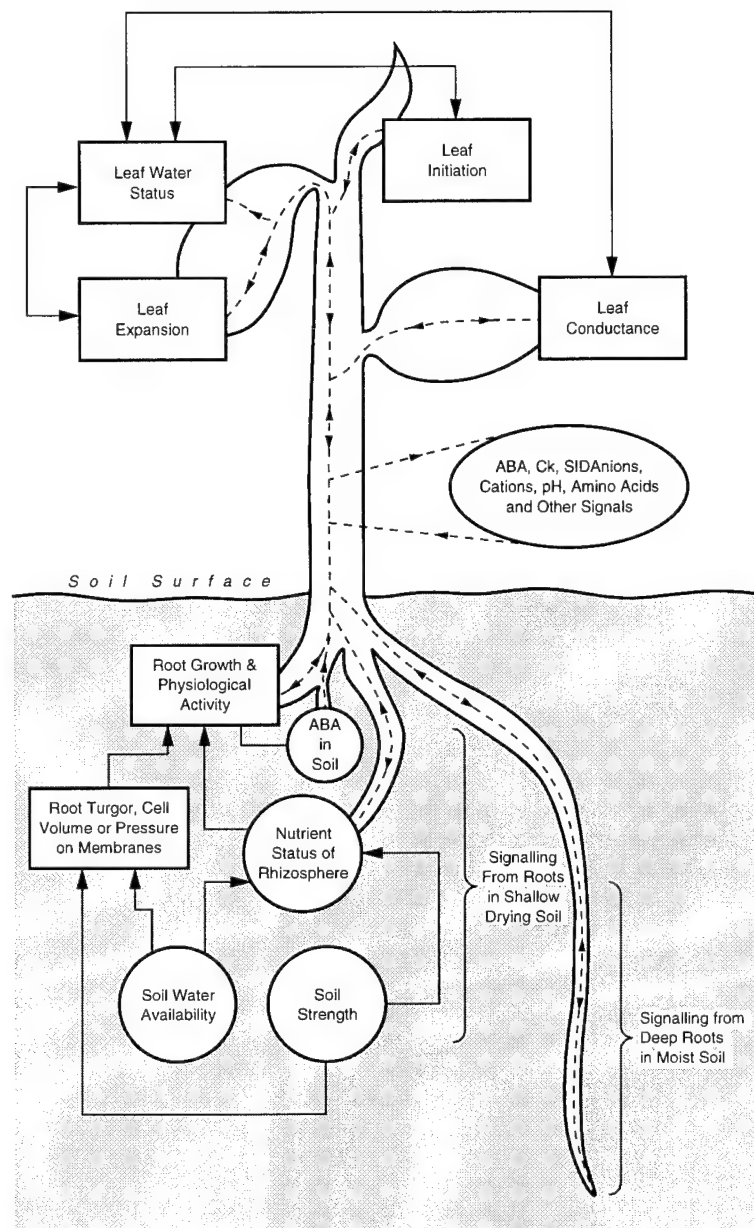
Figure 4. Factors influencing the generation of chemical information (dotted lines), soil effects (circles), plant physiological and developmental processes (rectangles) in roots in drying soils (after Davies and Zhang 1991).

form properties (Taylor 1983). A shallow root system with a high root density in the surface soil can result in rapid depletion of available water and nutrients, while a deep root system can make available a large volume of soil for root extraction of water and nutrients (Chaudhery and Sandhu 1983). A deeper root system is more efficient in water uptake compared with a shallow root system (Taylor and Klepper 1973).

In recent years, our understanding of the soil water flow through the soil–plant–air continuum has been strengthened by analogy with electrical engineering concepts such as the flow of electricity through a network of resistances (Fig. 5). Axial root resistance to water transport would increase in a deep root system (Meyer and Ritchie 1980); however, it is an insignificant component compared with radial resistance (Taylor and Klepper 1971). Feddes (1981) summarized plant resistances of various crops (Table 3). These data are empirical and can be applied to conditions from which they were derived. It is evident from the pub-

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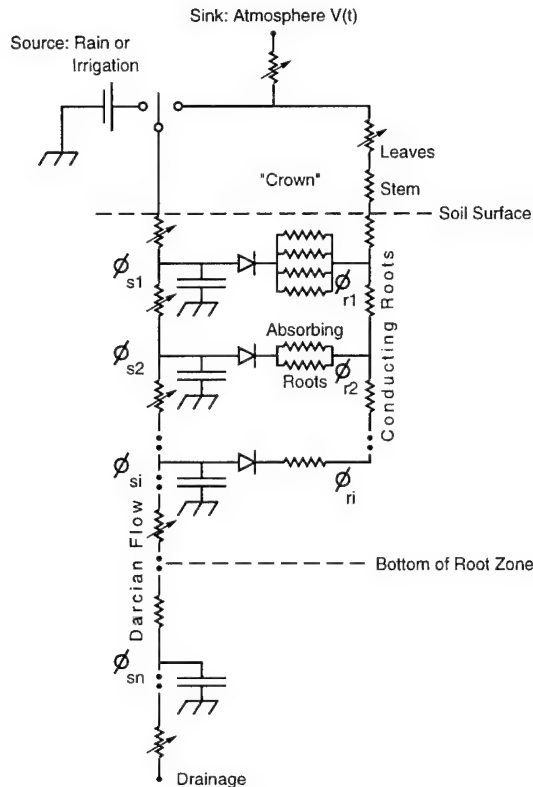
Figure 5. A root system in layered soil viewed as a resistance network. Water held in capacitors moves through variable resistance. Diodes permit flow into the roots but not from roots into the soil (after Hillel 1977).
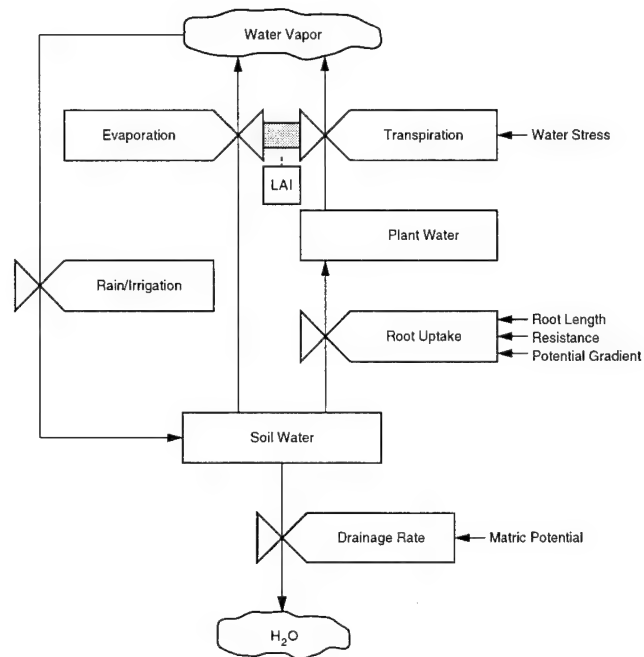
Figure 6. Water flow in the soil–root continuum. The "valve" symbols represent water flow rates between rectangular storage compartments or to external "sink" in the atmosphere or groundwater (after Huck and Hillel 1983).

Table 3. Plant resistance, R_p, data of various crops extracted from literature (after Feddes 1981).

Crop	Type of experiment	Root depth (cm)	R_p (10^3 cm)	Source
Birds foot trefoil	Lab	60	11.2	Gardner and Ehlig (1962)
Grass	Field	26	10.4	Rijtema (1965)
Potatoes	Field	40	10.3	Endrodi and Rijtema (1969)
Red cabbage	Field	42–82	31.4–36.3	Feddes (1971)
Wheat	Lab	45	9–21	Yang and de Jong (1971)
Wheat	Lab	18	31–58	Yang and de Jong (1972)
Italian ryegrass	Lab	22	5–17.5	Hansen (1974)
Maize	Greenhouse	—	13	Reicosky and Ritchie (1976)
Grain sorghum	Field	100	11	Reicosky and Ritchie (1976)
Douglas fir	Field	80	25	Nnyamah (1977)

lished literature that measurement of resistances encountered in the soil–root–plant system is still difficult or even impossible for many crops.

The pathway of water movement is from bulk soil to the rhizosphere, across the rhizosphere and the soil/root interface, across the cortex and the endodermis, and then into the lumen of the xylem. Water then moves along the xylem to the substomatal cavities where it undergoes a phase change to vapor and diffuses through the stomata and the leaf/air boundary layer. A generalized overview of macroscopic water flow processes is illustrated in Figure 6. Numerous water uptake models are published in the literature and can be classified as "macroscopic" or "microscopic."

Macroscopic models

Macroscopic models assume the vertical tran-

sient flow of water in a stable and uniform zone of soil. The root system is considered as a diffuse sink for water that permeates each depth of soil layer uniformly, though not necessarily at the same root length density through the root zone. Macroscopic models are derived from Darcy's law, expressed in hydraulic head terms

$$J_w = -K_w dH/dx \qquad (1)$$

where J_w = flux of water ($L^3 L^{-2} t^{-1}$)
$\qquad K_w$ = soil hydraulic conductivity ($L\ t^{-1}$)
$\qquad dH$ = hydraulic head difference (L)
$\qquad dx$ = distance along the flow path (L).

Incorporating the soil water diffusivity term, $D_w = K_w(d\Psi/d\theta)$, in eq 1

$$J_w = -D_w\ \partial\theta/\partial x. \qquad (2)$$

The vertical flow through a thin layer of soil where water content changes with time and distance can be solved with Richards (1931) continuity equation

$$\partial\theta/\partial t = \partial/\partial z\ K_w \partial H/\partial z + \partial K_w/\partial z$$

$$= \partial/\partial z\ D\partial\theta/\partial z + \partial K_w/\partial z. \qquad (3)$$

Equation 3 is further modified for water extraction by the plant roots

$$\partial\theta/\partial t = \partial\theta/\partial z\ (K_w \partial H/\partial z) + A_{(z,t)} \qquad (4)$$

where $A_{(z,t)}$ is the root water extraction in reference to soil depth, z, and time, t.

Several workers assumed that $A_{(z,t)}$ is a function of root activity. None, however, has assumed that root activity is a function of water potential difference between plant and soil, distance between the uniformly spaced roots, and some measure of conductivity in the root–soil system. The root water uptake model of Nimah and Hanks (1973) can be written as

$$A_{(z,t)} = H_{roots} + [RRES_{(z)}] - H_{(z,t)}$$

$$-S_{(z,t)} RDF_{(z)} Kw/\Delta x \Delta z \qquad (5)$$

where H_{roots} = effective water potential in root at $z = 0$
$\qquad RRES_{(z)}$ = root resistance equal to $1 + Rc$
$\qquad\qquad Rc$ = coefficient to account for longitudinal resistance in xylem

$H_{(z,t)}$ = soil matric potential
$S_{(z,t)}$ = soil osmotic potential
$RDF_{(z)}$ = proportion of total active roots in depth increments
$\qquad K_w$ = soil hydraulic conductivity at depth z
$\qquad \Delta x$ = distance between roots at position where $H_{(z,t)}$ and $S_{(z,t)}$ are measured
$\qquad \Delta z$ = soil depth increment.

The major drawback of these models is that they utilize a gross spatial average of matric and osmotic potentials and neglect the decrease in water potential and change in the salt concentration at the soil/root interface as well as the rhizosphere.

Microscopic models
Microscopic models consider the diffusion of water towards a single root (Gardner 1960). The models assume that liquid flow resistance in soil is dependent on root geometry, rooting length, and the hydraulic conductivity of the soil. Under steady-state conditions, the rate of water uptake per unit root length, q_r, from the soil at a uniform equilibrium water content can be estimated as

$$q_r = -2\Pi K_w[H_p - H_s]/\ln (r_{soil}/r_{root}) \qquad (6)$$

where K_w = soil hydraulic conductivity
$\qquad H_p$ = matric head in root epidermis or total leaf water potential
$\qquad H_s$ = matric head in soil surrounding root
$\qquad r_{soil}$ = radius of soil cylinder surrounding root
$\qquad r_{root}$ = root radius.

Root water uptake of a specific soil volume can be estimated by multiplying the q_r with root length density, L_v. The transpiration rate, T, is assumed to be equal to uptake rate and can be calculated as

$$T = \sum_i^1 q_{ri}\ L_{vi}. \qquad (7)$$

Taylor and Klepper (1975) proposed the following equation

$$\theta_{final} = \theta_{initial} - (q_r)\ (L_v)\ (H_p - H_s) \qquad (8)$$

where θ_{final} and $\theta_{initial}$ are the volumetric water contents at the end and beginning of a measuring period.

Water uptake rates of species differ even when

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Table 4. Specific water uptake rates for some tropical and temperate species (after Rendig and Taylor 1989).

Species	Water uptake rate ($m^3\,m^{-1}\,s^{-1}$)		Source
Cotton	5×10^{-12} to	5×10^{-11}	Bar-Yosef and Lambert (1981)
	$<1 \times 10^{-14}$ to	8×10^{-12}	Taylor and Klepper (1975)
Field pea	1×10^{-12} to	2×10^{-11}	Hamblin (1985)
Lupin	3×10^{-12} to	8×10^{-12}	Hamblin (1985)
Corn	3×10^{-12} to 2.4×10^{-10}		Allmaras et al. (1975)
	1×10^{-12} to 2.4×10^{-11}		Taylor and Klepper (1973)
Oats	8×10^{-12} to	1×10^{-10}	Ehlers et al. (1980)
Soybean	2×10^{-11} to	3×10^{-10}	Allmaras et al. (1975)
	2×10^{-12} to	3×10^{-10}	Willatt and Olsson (1982)
	2.8×10^{-11} to 2.2×10^{-10}		Willat and Taylor (1978)
Wheat	1×10^{-12} to	2×10^{-12}	Greacen and Hignett (1976)
Spring	4×10^{-13} to	1×10^{-12}	Hamblin (1985)
Winter	2×10^{-13} to	2×10^{-12}	Gregory et al. (1978)
Temperate grasses	about 1×10^{-12}		Welbank et al. (1974)
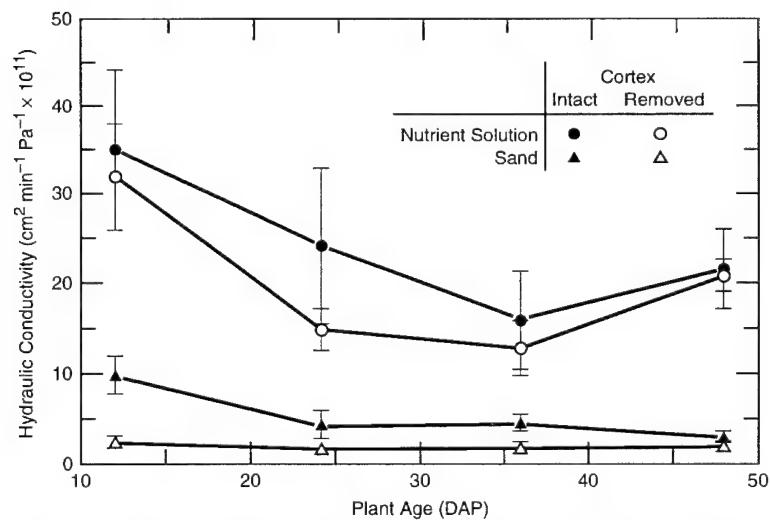
Figure 7. Effect of plant age on the hydraulic conductivity of hydroponically grown and sand-grown cotton roots (after Brar et al. 1990b).

they are grown under identical conditions (Table 4). For example, lupin and wheat were grown at the same location and time, yet their maximum uptake rates were 2×10^{-9} and 1×10^{-12} m^3 m^{-1} s^{-1}, respectively. Root uptake models often assume that hydraulic conductivity of the root system is a constant at all plant growth stages. Conversely, Brar et al. (1990b) reported that hydraulic conductivity of young cotton roots changed with plant age (Fig. 7). Hydraulic conductivity decreased 45% in nutrient solution-grown roots and 57% in sand-grown roots between 12 days after planting (DAP) to the mean

of the 24, 36, and 48 DAP. Hydraulic conductivity of sand-grown roots was 4 to 10 times lower than that for roots grown hydroponically, whether conductivity was compared at equal DAP or at equal root length (Table 5).

Nutrient uptake

Nutrient uptake is related to diversity in nutrient mobility in soil as well as the surface characteristics of the roots. Root length, root radius, and surface area are the important characteristics of the roots that determine the rate of nutrient up-

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Table 5. Total length of cotton as affected by plant age and root medium; hydroponic or sand (after Brar et al. 1990b).

Plant age*	Root length			
	Hydroponic (m)		Sand (m)	
12	3.3[†]	(1.0)**	2.6[a]	(0.7)
24	13.4[b]	(2.4)	14.4[b]	(2.9)
36	28.8[c]	(1.5)	17.4[b]	(4.9)
48	93.9[d]	(6.2)	17.1[b]	(2.6)

* Days after planting.
† Means with the same letter are not significantly different ($P < 0.05$).
** Standard error of mean.

take (Nye and Tinker 1969, Barber and Silberbush 1984). The relationship between solution concentration (c_i) of a given nutrient and its uptake by plant roots intact with the solution was proposed by Bouldin (1961) and modified by Nye (1966)

$$J = \alpha c_i \tag{9}$$

where J = rate of nutrient uptake (flux) expressed in terms of quantity per unit root area per unit time, and α = the proportionality term describing the root absorbing power.

If the term "uptake per unit root area" in the above equation is replaced with "root length,"

$$J = 2\Pi \alpha r c_i \tag{10}$$

where r = root radius. Nye and Tinker (1969) combined the terms α and r and provided a new term called root demand coefficient. For the evaluation of total uptake, they incorporated the total root length (L) in eq 10

$$J = 2\Pi \alpha r c_i L. \tag{11}$$

The soil and plant factors affecting the root demand coefficient are
1. Nutrient demand for plant growth;
2. Operation of metabolically driven uptake and transport mechanisms;
3. Functioning of physical and chemical processes in the root environment.

Mathematical models have been developed for nutrient uptake by plant roots (Nye and Marriott 1969, Nye et al. 1975, Claassen and Barber 1976, Barber and Cushman 1981, Tillotson and Wagenet 1982). These models help in understanding the complex soil–rhizosphere–root–plant system and in determining the significance of the parameters involved. The basic transport equation used in

the models to describe radial flux to the root by mass–flow and diffusion as affected by uptake by the root is

$$\frac{\partial c_i}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left[rD_c \frac{\partial c_i}{\partial r} + \frac{r_0 v_0 c_i}{b} \right] \tag{12}$$

where c_i = ion concentration in solution
r = radial distance from the root axis
r_0 = root radius
D_c = apparent diffusion coefficient
v_0 = flow velocity of soil solution to root
b = buffer capacity = $(\partial c_i/\partial t)/(\partial c_i/\partial r)$
t = uptake time.

Boundary conditions are required to find the solution to eq 12. The initial boundary condition of the equation is:

$$t = 0, \qquad r > r_0, \qquad c_i = c_{ii} \tag{13}$$

where c_{ii} = initial nutrient concentration in the soil solution.

The first boundary condition is

$$D_c b \frac{\partial c_i}{\partial t} + v_0 c_i = \frac{J_{max}(c_i - c_{min})}{K_m + (c_i - c_{min})} \quad \text{at } r = r_0, \ t > 0 \tag{14}$$

where $c_{min} = c_i$ when J_n = net flux is zero, K_m = Michaelis–Menten constant.

The second boundary condition, added by Cushman to account for competition between adjacent roots, is

$$D_c b \frac{\partial c_i}{\partial t} + v_0 c_i = 0, \qquad r = r_i, \qquad t > 0 \tag{15}$$

where r_i = mean half-distance between root axes. In the absence of competition, $c_i = c_{ii}$ at $r = r_i$ and $t > 0$.

Assumptions made in the Claassen-Barber model are
1. Soil is homogeneous and isotropic;
2. Root zone has constant soil water content that is maintained at field capacity;
3. Plant or root age has no impact on nutrient flux;
4. Nutrient concentration has no impact on convective component of flux;
5. Nutrients move to the root by diffusion and mass–flow processes; roots are considered as smooth cylinders that absorb nutrients from the soil solution as per Michaelis–Menten kinetics;
6. Apparent diffusion coefficient and buffer

capacity are independent of the nutrient concentration.

Parameters required for the Claassen-Barber model along with one additional parameter required for the Cushman model are

1. Root morphology
   a) Initial root length
   b) Rate of root growth
   c) Average root radius
2. Root uptake kinetics
   a) Maximum influx J_{max} of the nutrient
   b) External nutrient concentration K_m to obtain one-half J_{max}
   c) External nutrient concentration c_{min} where net nutrient uptake is nil
3. Soil nutrient supply
   a) Rate of water influx
   b) Concentration of the nutrient in the soil solution at the start of the plant growth period
   c) Apparent diffusion coefficient of the nutrient
   d) Differential soil buffer capacity b for the nutrient
   e) Mean half-distance between root axes

The Cushman–Barber model, written in Pascal and compiled for IBM PC, is available for educational purposes (Oates and Barber 1987).

ROOT GROWTH UNDER PHYSICAL EDAPHIC CONSTRAINTS

Soil water

The most crucial edaphic factor in a plant's life is water, which links it to the soil via roots and serves as a vehicle for nutrient transport. Water also controls the exchange of gases and moderates soil temperature changes (Clothier and Scotter 1985). Soil absorbs, stores, and releases water depending upon volume and size distribution of pores as determined by texture, structure, organic matter content, and the depth of the soil. Plant available water is held in the soil between –0.01 or –0.03 MPa potential (in coarse-textured and fine-textured soils, respectively), known as the upper limit or field capacity, and –1.5 MPa potential, called the lower limit or permanent wilting point. Water availability may not be limited to –1.5 MPa potentials; plant roots can extract water at lower potentials depending upon the plant type and the aerial environment (Musick et al. 1976).

Root growth rates are controlled by the presence of continuing supplies of water to maintain hydrostatic pressure in the elongating cells of the root, metabolites for cell wall construction, and growth hormone to loosen the bonds within the cell wall constituents (Lockhart 1965). Water flows radially into the elongating root cells only when the cell's total water potential is lower than the combined osmotic and matric potentials of the soil (Rendig and Taylor 1989). Furthermore, lowered soil water content can shrink root diameter (Cole and Alston 1974), which reduces root/soil contact, increases root senescence, lowers soil hydraulic conductivity, reduces the water potential of the soil surrounding a specific root, and decreases root hairs, thereby affecting the water and nutrient uptake.

Water absorption is influenced by the geometric distribution of viable roots in the soil profile and the availability of water at the root surfaces (Smucker and Aiken 1992). Absorption of soil water is not always linear with greater root growth. Incomplete root contact with the soil and/or declining soil water potentials reduce the water absorption efficiencies, resulting in the production of excessive plant root surfaces. Weak root contact with the soil matrix results as roots are clustered within the macropores of soils and smaller roots grow along soil aggregates or in pores larger than the diameter of the roots (Lafolie et al. 1991, van Noordwijk et al. 1992). Greater root/soil contact occurs as roots are exposed to a compacted soil environment (Kooistra et al. 1992).

Lascano and van Bavel (1984) calculated the partition of the water uptake rate over the root zone as

$$R_j = (\Psi_{sj} - \Psi_{e,i})RD_j/PHR \qquad (16)$$

where R_j = rate of water extraction from the root zone or compartment j
Ψ_{sj} = soil water potential in that compartment
$\Psi_{e,i}$ = effective leaf water potential
RD_j = relative root density in the soil compartment
PHR = specific plant resistance.

The summation of R_j from each soil compartment equals the total water uptake, provided there is no change in water content of the plant. In nature, this is not true because the plant water content changes diurnally with radiation load and changing soil water content. Lascano and van Bavel also assumed that the plant hydraulic resistances are constant; conversely, the significance of plant

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resistance in water transport was reported by Van den Honert (1948). Under steady-state conditions, the pathway of water movement through the soil–root–stem–leaves could be expressed as resistances in series (Fig. 5) using the equation

$$T = \Psi_s - \Psi_r/R_s = \Psi_r - \Psi_l/R_p \qquad (17)$$

where T = transpiration rate, Ψ_s, Ψ_r, and Ψ_l are the water potentials in the soil matrix, at the root surface, and in the leaves, respectively; and R_s and R_p are resistances of the soil and plant pathways. R_p is considered to be dominant over R_s and decreases with increased transpiration rate (Feddes 1981).

Steady-state conditions rarely exist in the field. Furthermore, the plant root system is dynamic (root senescence occurs and new roots emerge), root geometry is time-dependent, and water permeability varies with position along the root and with time. Instead of considering water flow to single roots, a more suitable approach might be the macroscopic one, in which a sink term representing water extraction by a homogeneous and isotropic element of the root system (volume of water per volume of soil per unit of time) is added to the conservation mass equation (eq 4).

Variation in root diameter has long been observed, which further complicates the mathematical analysis of root function. Models of the transport of ions, water, oxygen, and other materials from the soil to the root interior assume the root has constant diameter, and transfer coefficients remain constant with time.

The simulation of water transport through a root system is complicated in cold regions because of the presence of permafrost and seasonally frozen soils. Furthermore, the soil freezing front and ice formed in the frozen ground enhance runoff and reduce groundwater recharge. A few workers (Taylor and Luthin 1978, Guymon et al. 1980, Hromadka et al. 1981) studied the complex processes of characterizing simultaneous heat and soil water transport in a freezing soil without considering vegetation. The physics of a frozen heterogeneous soil profile include the terms of the soil energy balance and soil water balance. The one-dimensional energy conservation equation for potentially freezing soils can be written as

$$\partial/\partial z\left[\hbar(\theta)\partial T/\partial z\right] + \rho_\ell c_\ell\left(\partial v_\ell T/\partial z\right) + S_h = C_s\partial T/\partial t$$

$$- \rho_i L_f\left(\partial\theta_i/\partial t\right) + L_v\left(\partial\rho_v/\partial t + \partial\vartheta v/\partial z\right).$$

The mass conservation equation can be written as

$$\partial/\partial z\left[K(\theta)(\partial h_m/\partial z + 1)\right] + \partial\vartheta_v/\rho_\ell\partial z + Sm$$

$$= \partial\theta/\partial t + \rho i\partial\theta i/\rho 1\partial t \qquad (19)$$

where ρ_ℓ = density of liquid water
c_ℓ = specific heat capacity of water
v_ℓ = downward liquid water flux
C_s = volumetric heat capacity of soil
ρ_i = density of ice
L_f = latent heat of fusion
θ_i = volumetric ice content
ρ_v = vapor density in soil pore space
ϑv = downward water vapor flux through soil
S_h = heat sink/source
Sm = water sink/source
θ = volumetric soil water content
t = time
T = temperature
z = soil depth
$\hbar$ = thermal conductivity of soil.

Several other workers used eq 18 and 19 and developed the following types of water transport models (Kung and Steenhuis 1986).
1. Models based on an analogy between the mechanism of water transport in unsaturated soil and in frozen soil (Harlan 1971).
2. Models based on the theory that the pressure jump is due to the curvature in the liquid water/ice/air interfaces (Bresler and Miller 1975; Miller 1973, 1977, 1978; Miller et al. 1975).
3. Models based on the theory of irreversible thermodynamics (Kay and Groenevelt 1974, Groenevelt and Kay 1974, O'Neill and Miller 1982).
4. Models simulating temperature distribution in a partially frozen soil (Miller et al. 1984).

These models were developed without considering the plant root system. During thawing season, soils without vegetation in cold regions are susceptible to degradation processes of soil erosion, nutrient losses, and organic matter depletion.

Soil air

Roots and soil organisms capture energy from the oxidation of organic substances in a series of enzyme-catalyzed reactions. Plants need molecular oxygen to respire and convert carbohydrates to carbon dioxide and water. This is an exother-

mic reaction and releases respiratory energy that is utilized for many plant processes. The disappearance of molecular oxygen triggers a sequence of changes in the physico-chemical properties of the soil (Gambrell and Patrick 1978, Ponnamperuma 1984). Such changes include accumulations of reduced metal ions, organic acids, and volatiles that are potentially harmful to plant roots (Drew and Lynch 1980). Such accumulation to phytotoxic levels requires time. The absence of oxygen alone is sufficient to profoundly alter the plant metabolism (Drew 1983).

In cold climates, cool autumn or early spring temperatures result in a slow rate of depletion of dissolved soil oxygen by respiration of roots and soil organisms (Drew 1992). The root apical meristem, the zone of fastest oxygen consumption, is particularly sensitive to oxygen deficiency and the sequence of metabolic events leading to cell death (Roberts et al. 1984a,b). In summer, crops of cold climates consumed oxygen at the rate of 1.7 L m^{-3} day^{-1}; furthermore, oxygen consumption rates reduce to 1.5 L m^{-3} day^{-1} in winter, and to about half in the absence of plants (Currie 1970).

Suboptimal oxygen concentrations in the soil air occur because of interactions among soil properties such as porosity, water content, temperature, surface water movement, and continuity of air-filled pores with biotic activity (Drew 1983, Grable 1966). Jones et al. (1991) developed a root growth simulation model and considered the effect of soil water content, bulk density, texture, and plant genotype on soil air. Increased soil water content or bulk density reduce the oxygen diffusion rate and affect air-filled porosity. The diffusion coefficient of oxygen in air is approximately 10,000 times greater (0.23 cm^2 s^{-1}) than that in water (0.26 × 10^{-4} cm^2 s^{-1}) at 26°C (Rendig and Taylor 1989).

A mathematical model for the relationship of root respiration, soil oxygen supply, and internal oxygen supply was first developed by Luxmoore et al. (1970). Measurements used to predict the effect of a reduced soil oxygen supply on root growth and function are
1. Oxygen diffusion rate;
2. Oxygen concentration in the soil;
3. Air-filled porosity percentage;
4. Redox potential;
5. Air permeability.

Soil air that is low in oxygen can contain high concentrations of ethylene, which is a growth regulator rather than a toxin. Elevated concentration of ethylene inhibits root elongation, cambial activity, and stellar differentiation in roots (Rendig and Taylor 1989). An ethylene concentration of ≤ 0.4 ppm can inhibit nodule formation on legume roots. Furthermore, ethylene has some advantageous impact on roots and stimulates lateral branching as well as root hair initiation (Rendig and Taylor 1989).

Soil temperature

Temperature influences plant processes at the cellular level, such as osmotic potential, hydration of ions, stomatal activity and transpiration, Gibbs free energy available for work, membrane permeability, solute solubilities, diffusion, and enzymatic activities (Voorhees et al. 1981). The final shape of the root system is determined from root branching and elongation of individual root axes. Several reviews indicate that most plant species exhibit an optimum temperature for maximum root elongation rates (Nielson and Humphries 1966, Cooper 1973). Furthermore, the species within a genus (Heinrichs and Nielsen 1966) and cultivars within a species (Johnson and Hartman 1919) varied in root elongation and branching rates in response to temperature. For instance, Brar et al. (1990a) reported high variability among legume cultivars in main axis root length at different specific temperatures (Fig. 8).

Low temperature reduces water absorption by increasing the water viscosity and decreasing cell membrane permeability. Furthermore, low temperatures also decrease metabolic activity and decrease the root growth (dry matter production). The addition of fertilizer, particularly phosphorus, may compensate to some extent for the reduced growth in cold soils (Nielsen and Humphries 1966).

Snow cover has a large influence on soil temperature. Snow cover decreases heat conduction to the soil surface (Legget and Crawford 1952) and serves as a sink for heat fluxes at both upper and lower surfaces of the cover (Granger et al. 1977). Relationships between air temperature and snow depth can be used to predict the minimum soil temperatures (Fig. 9). The pattern of seasonal warming of air temperature is predominantly temporal at the ground surface; however, its effect is temporal as well as spatial below ground and causes temperature limitations on root growth (Fig. 10). During the growing season, as the warming front moves downward, temperatures of the deeper soil layers become suitable for root growth. The depth of soil thermally suitable for appreciable root growth is a function of both
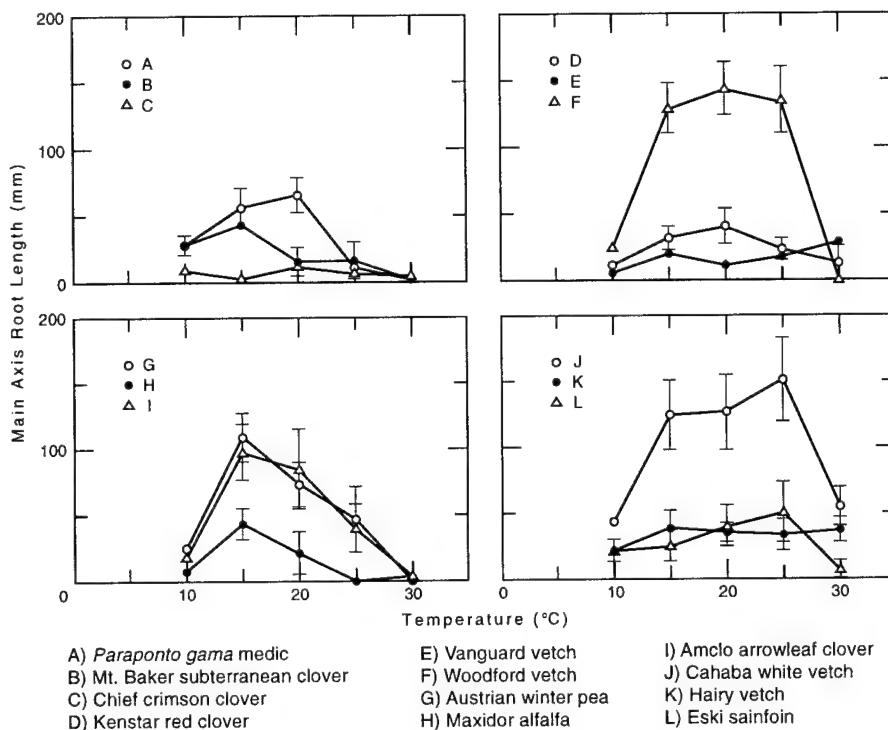
Figure 8. Main axis root length at ten days after planting as a function of temperature (after Brar et al. 1990a).

A) *Paraponto gama* medic
B) Mt. Baker subterranean clover
C) Chief crimson clover
D) Kenstar red clover
E) Vanguard vetch
F) Woodford vetch
G) Austrian winter pea
H) Maxidor alfalfa
I) Amclo arrowleaf clover
J) Cahaba white vetch
K) Hairy vetch
L) Eski sainfoin
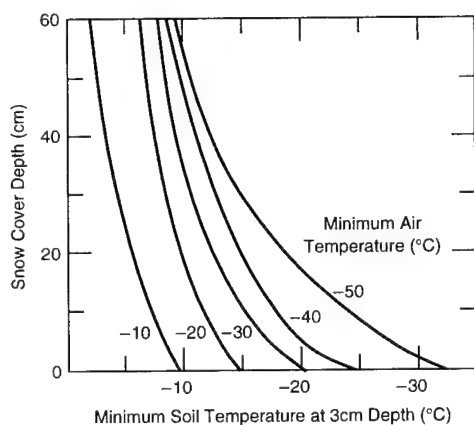
Figure 9. Minimum soil temperature at 3-cm depth as affected by minimum air temperature and depth of snow cover (after Shul'gin 1967).

Figure 10. Seasonal warming of air temperatures (5-year average of daily means) determines when temperatures are favorable for plant growth. Soil temperatures favorable for root growth vary with time and depth (modeled thermal regime) (after Kasper and Bland 1992).

soil temperature regimes and root temperature response (Kaspar and Bland 1992).

Soil temperature usually limits root system expansion and proliferation. Root expansion is a function of temperature-dependent processes such as growth and development. Growth processes include cell elongation, root length increase, and root diameter. Developmental processes generally control growth duration of cells (Burstrom 1956, Beauchamp and Lathwell 1966),

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organs, and whole plants (Beauchamp and Lathwell 1967). The number of lateral roots, distance from a root tip to first visible lateral root, lateral root density, root hairs, and root plagiotropism (growth at angles from the vertical) are temperature-sensitive (Atkin et al. 1973, Engels et al. 1992, Mozafar and Oertli 1992).

Root dry weight is the most commonly measured parameter that follows a typical growth response curve (Cooper 1973). Root length, surface area, and extension of roots into deeper soil layers are important parameters that influence water and nutrient uptake. Present technology has the capability to measure these parameters. Root diameter is another important parameter influenced by temperature; it substantially reduces water and nutrient uptake (Barber et al. 1989) as well as the amount of carbohydrates required for root growth (Fitter 1991).
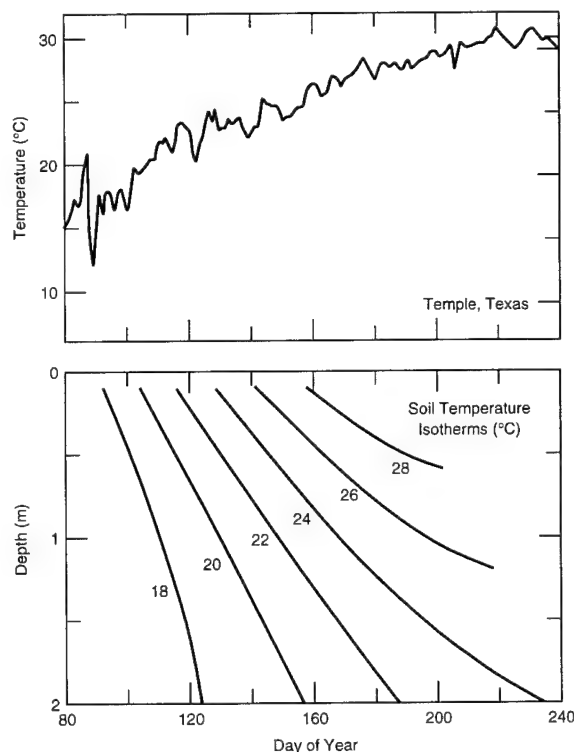
Most plant growth models related to water and nutrient transport require soil temperature with depth as input for the model. Temperature simulation models published in the literature are
1. Mechanistic models that need detailed initial and boundary inputs (Richtmeyer and Morton 1967, Wierenga and DeWit 1970, Hanks et al. 1971, Rosema 1975, Van Bavel and Hillel 1976, Grant et al. 1990);
2. Functional models that require weather station information and soil information at one depth (Neild 1971, Hasfurther and Burman 1974, Cruse et al. 1980, Gupta et al. 1984, Parton 1984, Brar and Unger 1994);
3. Statistical models of a regression type that were developed at a particular site from a limited data set (Meikle and Treadway 1979, Ghuman and Lal 1983, Langholz 1989, Dwyer et al. 1990).

The timing of snowmelt and above-freezing temperatures are the major factors controlling the onset of plant growth. Root elongation begins as soon as the soil is thawed and elongation is possible, depending on the depth of the individual root tips.

Physical impedance

Physical impedance, sometimes called mechanical impedance or excessive soil strength, can severely affect normal root growth patterns. Such impedances result from increased soil bulk density, increased cohesion between soil particles, increased friction between soil particles, reduction in soil water content, frost-heave action of soil, and presence of permafrost within the root zone. The
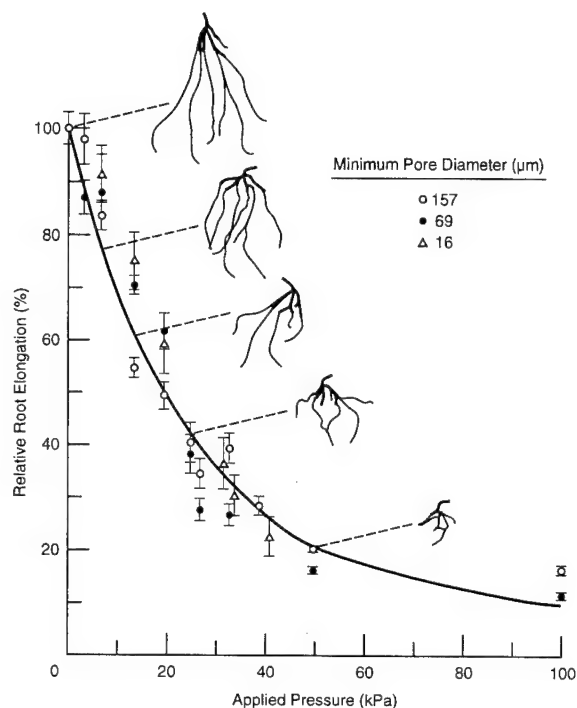
Figure 11. Effects of pressure applied to the outside surface of a flexible container on relative root elongation and shape of barley roots (after Russell and Goss 1974).

adverse physical impedances can severely affect the plant's ability to emerge from crusted soils, to extend its root system into unexplored soil volumes, to transport photosynthates from shoots to roots, and to transport water from roots to shoots. These impedances restrict below-ground expansion of root crops, e.g., turnip, sugar beet, or radish.

Under an excessive soil strength environment, roots enter the soil volume where pore sizes are larger than the root tip. Conversely, if the pore sizes are too small for the entry of the main root but not for laterals, then laterals proliferate and produce a highly branched root system (Russell and Goss 1974). Furthermore, if the pore sizes are too small and prevent entry of laterals, a stunted root system can result. Maximum pressures that roots can exert on the surrounding soil matrix range from 900 to 1500 kPa. Different species exert different maximum root growth pressures (Taylor 1983). The impeded roots are thicker in diameter and distorted in shape (Fig. 11).

Physical impedances result from
1. Natural consolidation during soil forming processes;
2. Trampling by animals, including humans;
3. Natural shrinkage of soils upon drying;
4. Soil response to pressures and deformations imposed by vehicle wheels;

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5. Actions of overburden and water droplets on water-weakened aggregates during rainfall;
6. Frost heave actions.

Physical impedance can be measured with penetrometers, shear vanes, shear rings, triaxial shear cells, and unconfined compression cells. As far as we know, no mathematical model is available to predict soil yielding under load using fundamental parameters.

Spatial variability

Considerable research has been reported in the literature during the past decade on the spatial variability of soil physical properties. However, in cold environments a computer literature search has revealed limited published studies on the spatial variability of solute and temperature, and none with respect to root water uptake. Therefore, this section is limited to reporting solute and temperature-related variability studies from cold environments.

Spatial variability has a significant effect on field-scale solute movement through the unsaturated zones. The effect of spatial variability in soil hydraulic properties has been investigated using either parametric models (Dagan and Bresler 1979, Bresler and Dagan 1981, Amoozegar-Fard et al. 1982, Simmons 1982, Destouni and Cvetkovic 1989) or transfer function models (Jury et al. 1986, Butters and Jury 1989). Few workers studied the temperature spatial variability in relation to soil water content (Vauclin et al. 1982, Davidoff et al. 1986).

OVERVIEW OF ROOT GROWTH MODELS

Several root growth models were developed during the past decade, but none is geared to the problems associated with root growth in cold regions. The models reported in the literature are classified as simple models, carbon-partition models, growing degree day-based models, soil parameter-based models, and arctic plant growth models.

Simple models

Root distribution with depth

The model of Gerwitz and Page (1974) is empirical in nature and simulates root density as a function of soil depth. The model makes no attempts to define the relative age classes of the individual root axes in each layer or the proportion of those axes that are first- or second-order laterals.

Root depth with time

Borg and Grimes (1986) developed a model to simulate actual root depth as a function of time. For a given crop and location, the model requires an estimate of the maximum rooting depth to be achieved and the number of days to reach maturity.

Root depth with temperature

The model is two-dimensional and was developed from data that explain the effect of root zone temperature on soybean root development (Stone et al. 1983). The model predicts the extension of the taproot and ten primary lateral roots for two groups of soybean cultivars. The simulation emphasizes the importance of soil temperature, but ignores many other factors responsible for root elongation.

Carbon partition models

Carbon partition models are complex compared to simple models. These models partition carbon between the above- and below-ground biomass. The partitioning coefficient is assumed to be a constant fraction of the daily photosynthetic production. Following are a few examples of carbon partition models.

Root:shoot ratios

Numerous studies have shown that plants tend to adjust their root:shoot ratio to maintain an internal carbon-nitrogen balance favorable for growth (Davidson 1969, Reynolds and Thornley 1982, Skiles et al. 1982, Johnson 1983, Coughenour et al. 1984, Fishman et al. 1984). Davidson (1969) developed a model based on a hypothesis that a functional balance exists between the size and activity of the shoot (which supplies carbohydrates) and the size and activity of the root (which supplies water and essential nutrients). His model suggested the partitioning of photosynthates.

Partition models were reviewed by Reynolds and Thornley (1982). They developed a model based on the assumption that the partition of new growth is controlled by whole-plant substrate concentrations. Their model partitioned the photosynthates between root and shoot on the basis of the nitrogen:carbon ratio in the plant's labile pool. In spite of good features and the high complexity of the model, however, it has the following drawbacks:

1. The carbon:nitrogen (C:N) substrate concentration ratio is always considered a fixed value not influenced by the external environment;

2. The model is unstable in terms of balanced growth;
3. The estimation of model parameters may pose considerable experimental difficulties.

The drawbacks of the Reynolds and Thornley model were corrected by Johnson (1983). His model is based on the partition of new growth between shoot and root in terms of carbon or nitrogen substrate levels and the shoot:root ratio. The model considers the partitioning parameters and dynamic responses to changing environment and root- and shoot-specific growth rates.

Grass crop model

Johnson and Thornley (1985) developed a model that divides root structure into four categories: growing, newly expanded, medium-aged, and senescencing roots.

SimRoot

SimRoot is a four-dimensional (i.e., space and time) data structure model developed by Davis (1993) and used by Nielsen et al. (1994) to simulate root growth based on types of root branches, branching angles, growth velocities of specific types of branches, spatial distribution of respiration, carbon exudation, and biomass along root axes. They emphasized the importance of considering root architecture in relation to nutrient acquisition efficiency and environmental factors, such as elevated CO_2 concentration that affects below-ground allocation of carbon resources.

Growing degree day-based models

WHTROOT (Porter et al. 1986), a winter wheat root growth model, was developed based on cumulative thermal time with descriptions of the extension and branching of individual age classes of seminal and crown root axes. The model requires sowing date and average monthly mean air temperature as input parameters. Model output provides maximum depth of penetration of each age class of root and root length density or root weight in any 10-cm layer of soil contributed by main axes, first order, and second order laterals on any calendar date.

Soil parameter-based models

Root growth model

Jones et al. (1991) developed a root growth model that simulates daily root growth of crops grown in a layered soil. Model input parameters are aluminum toxicity, calcium deficiency, coarse fragments, qualitative constraints, strength, aeration, and temperature. The authors claim that the model will work for mineral soils of temperate regions. However, the model does not account for soil situations such as variable-charge ion exchange capacity, wetness-dependent bulk density, soil fertility effect on root growth, freeze–thaw impact on root growth, and root water uptake in temperate climates.

ROOTMAP

ROOTMAP is a three-dimensional model to describe the growth and structure of fibrous root systems (Diggle 1988). Root growth is described in terms of growing time, number of axes, initiation time of axes, growth rate and branching characteristics of the roots, and characteristics governing the direction of root growth. A root system can be regarded as the result of the accumulated effects of growth and branching responses of individual root tips, the root tissues behind these root tips, local soil conditions, and overall state of the plant. The drawback of this model is that it cannot simulate the entire root system of a mature plant.

Bengough et al. (1992) modified the ROOTMAP model to allow the numerical output of the data on root intersections with horizontal and vertical planes.

Arctic plant growth models

Numerous whole-plant growth models for vascular and nonvascular plants have been developed for arctic ecosystems. Reynolds and Leadley (1992) reviewed 21 models based on a minimal set of processes and variables that are critical to predict plant growth under changing climatic conditions. Most of these models either ignored the roots or provided limited information on root growth simulation. Reynolds and Leadley found greater variability in whole-plant growth simulations. They classified these models into four general categories based on degree of mechanism and comprehensiveness: 1) budget, 2) flux, 3) semimechanistic, and 4) mechanistic (Fig. 12).

Budget models are empirical in nature and ignore any kind of mechanism or comprehensiveness. These models describe plant growth as the difference between input and output parameters. In addition, budget models treat plants as "black boxes" where plant biomass is lumped into a single box. Semimechanistic models contain low to medium comprehensiveness. The plant growth is described with a minimum number of components, and heavy emphasis is placed on phenologi-
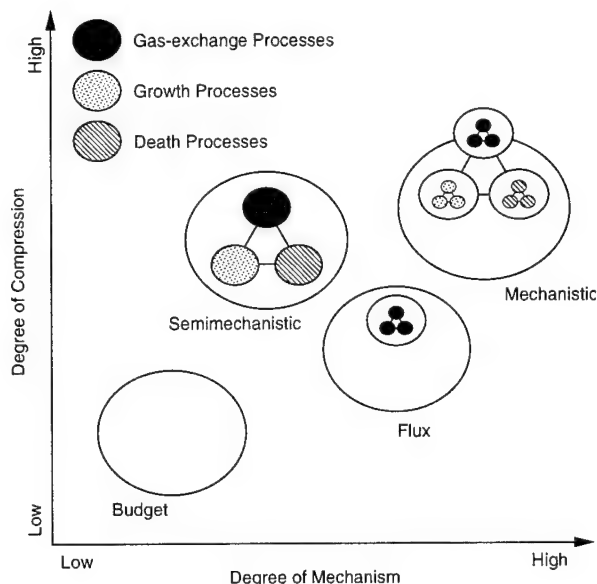
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Figure 12. Types of arctic plant growth models based on relative degree of comprehensiveness and mechanism. Comprehensiveness refers to the number of processes considered (e.g., gas exchange, growth, and death), whereas mechanism refers to the level of detail at which each of these processes is treated (after Reynolds and Leadley 1992).

cal modeling. Mechanistic models are based on the high mechanism and comprehensiveness that provide very detailed information. Flux models are a special kind of semimechanistic model. The models contain a high degree of mechanism and comprehensiveness in terms of gas exchange per se, but tend to have low overall comprehensiveness in terms of other plant growth processes.

It is evident from the literature reviewed that whole plant models combine mechanistic principles with empirical observations to predict mass as a function of various edaphic factors. Root uptake is usually treated in a highly simplified submodel, the root system acting as a zero-sink for nutrients, and the uptake is controlled by soil water potential and transpiration rate or by diffusion flux rate.

CONCLUSIONS

Our understanding of the fundamental aspects of growth and proliferation of plant roots within the temperate soil environment is incomplete. During the last seven or eight years, concepts of plant-water relations in dry soil have changed and consider the roots rather than the shoots to regulate plant growth and development. Recent evidence suggests that root signals

influence stomatal behavior and regulate leaf initiation, leaf expansion, and other development processes.

LITERATURE CITED

Allmaras, R.R., W.W. Nelson and W.B. Voorhees (1975) Soybean and corn rooting in southwestern Minnesota. II. Root distribution and related water inflow. *Soil Science Society of America Proceedings,* **39**: 771–777.

Amoozegar-Fard, A., D.R. Nielsen and A.W. Warrick (1982) Soil solute concentration distributions for spatially varying pore water velocities and apparent diffusion coefficients. *Soil Science Society of America Journal,* **46**: 3–8.

Atkin, R.K., G.E. Barton and D.K. Robinson (1973) Effect of root-growing temperature on growth substances in xylem exudate of *Zea mays. Journal of Experimental Botany,* **24**: 475–487.

Barber, S.A. (1978) Growth and nutrient uptake of soybean roots under field conditions. *Agronomy Journal,* **70**: 457–461.

Barber, S.A. and J.H. Cushman (1981) Nitrogen uptake model for agronomic crops. In *Modeling Wastewater Renovation-Land Treatment* (I.K. Iskandar, Ed.). New York: Wiley-Interscience, p. 382–409.

Barber, S.A. and M. Silberbush (1984) Plant root morphology and nutrient uptake. In *Roots, Nutrient and Water Influx and Plant Growth* (D.M. Kral, Ed.). American Society of Agronomy, Madison, Wisconsin, ASA Special Pub. No. 49, p. 65–87.

Barber, S.A., A.D. Mackay, R.O. Kuchenbuch and P.B. Barraclough (1989) Effects of soil temperature and water on maize root growth. *Developments in Plant Soil Science,* **36**: 231–233.

Barley, K.P. (1970) The configuration of the root system in relation to nutrient uptake. *Advances in Agronomy,* **22**: 159–201.

Barraclough, P.B. (1989) Root growth, macronutrient uptake dynamics and soil fertility requirements of a high-yielding winter oilseed rape crop. *Plant Soil,* **119**: 59–70.

Barraclough, P.B., H. Kuhlmann and A.H. Weir (1989) The effects of prolonged drought and nitrogen fertilizer on root and shoot growth and water uptake by winter wheat. *Journal of Agronomy and Crop Science,* **163**: 352–360.

Barraclough, P.B., A.H. Weir and H. Kuhlmann (1991) Factors affecting the growth and distribution of winter wheat roots under UK field conditions. In *Plant Roots and Their Environment. Proceedings of the International Society of Root Research*

Symposium, 21–26 August 1988, Uppsala, Sweden (B.L. McMichael and H. Persson, Ed.). New York: Elsevier, p. 410–417.

Bar-Yosef, B. and J.R. Lambert (1981) Corn and cotton root growth in response to soil impedance and water potentials. *Soil Science Society of America Journal,* **45**: 930–935.

Beauchamp, E. and D.J. Lathwell (1966) Root-zone temperature effects on the vascular development of adventitious roots in *Zea mays. Botanical Gazette,* **127**: 153–158.

Beauchamp, E. and D.J. Lathwell (1967) Root-zone temperature effects on the early development of maize. *Plant Soil,* **26**: 224–234.

Bengough, A.G., C.J. Mackenzie and A.J. Diggle (1992) Relations between root length densities and root intersections with horizontal and vertical planes using root growth modelling in 3 dimensions. *Plant Soil,* **145**: 245–252.

Billings, W.D (1992) Phytogeographic and evolutionary potential of the arctic flora and vegetation in a changing climate. In *Arctic Ecosystem in a Changing Climate* (F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda, Ed.). New York: Academic Press, p. 91–109.

Borg, H. and D.W. Grimes (1986) Depth development of roots with time: An empirical description. *Transactions of the American Society of Agricultural Engineers,* **29**: 194–197.

Bouldin, D.R. (1961) Mathematical description of diffusion processes in the soil-plant system. *Soil Science Society of America Proceedings,* **25**: 476–480.

Brar, G.S. and P.W. Unger (1994) Soil temperature simulation with varying residue management. *Journal of Agronomy and Crop Science,* **172**: 1–8.

Brar, G.S. and A.J. Palazzo (1995) Shoot and root development of tall and hard fescues in two different soils. *Journal of Environmental Quality,* **24**: 777–781.

Brar, G.S., J.F. Gomez, B.L. McMichael, A.G. Matches and H.M. Taylor (1990a) Root development of 12 forage legumes as affected by temperature. *Agronomy Journal,* **82**: 1024–1026.

Brar, G.S., B.L. McMichael and H.M. Taylor (1990b) Hydraulic conductivity of cotton roots as influenced by plant age and rooting medium. *Agronomy Journal,* **82**: 264–266.

Brar, G.S., J.L. Steiner, P.W. Unger and S.S. Prihar (1992) Modeling sorghum seedling establishment from soil wetness and temperature of drying seed zones. *Agronomy Journal,* **84**: 905–910.

Bresler, E. and R.D. Miller (1975) Estimation of pore blockage induced by freezing of unsaturated soil. In *Proceedings of Conference on Soil Water Problems in Cold Regions, Calgary, Alberta, Canada, 6–7 May,* p. 161–175.

Bresler, E. and G. Dagan (1981) Corrective and pore scale dispersive solute transport in unsaturated heterogeneous fields. *Water Resources Research,* **17**: 1683–1693.

Brown, K.F. and P.V. Biscoe (1985) Fibrous root growth and water use of sugar beet. *Journal of Agricultural Science,* **105**: 679–691.

Burstrom, H. (1956) Temperature and root cell elongation. *Plant Physiology,* **9**: 682–692.

Butters, G.L. and W.A. Jury (1989) Field scale transport of bromide in an unsaturated soil. 2. Dispersion modeling. *Water Resources Research,* **25**: 1583–1589.

Chaudhery, T.N. and K.S. Sandhu (1983) Soil physical environment and root growth. *Advances in Soil Science,* **1**: 1–43.

Claassen, N. and S.A. Barber (1976) Simulation model for nutrient uptake from soil by a growing plant root system. *Agronomy Journal,* **68**: 961–964.

Clothier, B.E. and D.R. Scotter (1985) Water and solute movement in the root zone. *New Zealand Agricultural Science,* **19**: 187–192.

Cole, P.J. and A.M. Alston (1974) Effect of transient dehydration on absorption of chloride by wheat roots. *Plant Soil,* **40**: 243–247.

Cooper, A.J. (1973) Root temperature and plant growth–A review. Commonwealth Bureau of Horticulture and Plantation Crops, Commonwealth Agriculture Bureau, Farnham Royal, England, Research Review No. 4, p. 73.

Coughenour, M.B., S.J. McNaughton and L.L. Wallace (1984) Modelling primary production of perennial graminoids-uniting physiological processes and morphometric traits. *Ecological Modeling,* **23**: 101–134.

Cruse, R.M., D.R. Linden, J.K. Radke, W.E. Larson and K. Larentz (1980) A model to predict tillage effects on soil temperature. *Soil Science Society of America Journal,* **44**: 378–383.

Currie, J.A. (1970) Movement of gases in soil respiration. In: Sorption and transport processes in soils. *Society of Chemical Industry Monographs,* **37**: 152–171.

Dagan, G. and E. Bresler (1979) Solute dispersion in unsaturated heterogeneous soil at a field scale. I. Theory. *Soil Science Society of America Journal,* **43**: 461–467.

Davidoff, B., J.W. Lewis and H.M. Selim (1986) A method to verify the presence of a trend in studying spatial variability of soil temperature. *Soil Science Society of America Journal,* **50**: 1122–1127.

Davidson, R.L. (1969) Effect of root-leaf tempera-

ture differentials on root/shoot ratios in some pasture grasses and clover. *Annals of Botany*, **33**: 561–569.

Davies, W.J. and J. Zhang (1991) Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Plant Molecular Biology*, **42**: 55–76.

Davis, R.D. III (1993) Geometric modelling and computer visualization of botanical root systems. M.S. Thesis, Pennsylvania State University.

Destouni, G. and V. Cvetkovic (1989) The effect of heterogeneity on large scale solute transport in the unsaturated zone. *Nordic Hydrology*, **20**: 43–52.

Diggle, A.J. (1988) ROOTMAP – A model in three-dimensional coordinates of the growth and structure of fibrous root systems. *Plant and Soil*, **105**: 169–178.

Drew, M.C. (1983) Plant injury and adaptation to oxygen deficiency in the root environment: A review. *Plant Soil*, **75**: 179–199.

Drew, M.C. (1992) Soil aeration and plant root metabolism. *Soil Science*, **154**: 259–268.

Drew, M.C. and J.M. Lynch (1980) Soil anaerobiosis, micro-organisms and root functions. *Annual Reviews of Phytopathology*, **18**: 37–66.

Dwyer, L.M., H.N. Hayhoe and J.L.B. Culley (1990) Prediction of soil temperature from air temperature for estimating corn emergence. *Canadian Journal of Plant Science*, **70**: 619–628.

Ehlers, W., B.K. Khosla, U. Kopke, R. Bohm and K. Baeumer (1980) Tillage effects on root development, water uptake and growth of oats. *Soil Tillage Research*, **1**: 19–34.

Endrodi, G. and P.E. Rijtema (1969) Calculation of evapotranspiration from potatoes. *Netherlands Journal of Agricultural Science*, **17**: 283–299.

Engels, C., L. Munkle and H. Marschner (1992) Effect of root zone temperature and shoot demand on uptake and xylem transport of macronutrients in maize (*Zea mays* L.). *Journal of Experimental Botany*, **43**: 537–547.

Feddes, R.A. (1971) Water, heat and crop growth. Thesis Comm. Agricultural University of Wageningen, 71-12, p. 184.

Feddes, R.A. (1981) Water use models for assessing root zone modification. In *Modifying the Root Environment to Reduce Crop Stress* (G.F. Arkin and H.M. Taylor, Ed.). American Society of Agricultural Engineering, St. Joseph, Missouri, p. 347–390.

Fishman, S., H. Talpaz, M. Dinar, M. Levy, Y. Arazi, Y. Rozman and S. Yarshowsky (1984) A phenomenological model of dry matter partitioning among plant organs for simulation of potato growth. *Agricultural Systems*, **14**: 159–169.

Fitter, A.H. (1991) Characteristics and function of root systems. In: *Plant Roots: The Hidden Half* (Y. Waisel, A. Eshel and U. Kafkafi, Ed.). New York: Marcel Dekker, p. 3–24.

Gambrell, R.P. and W.H. Patrick (1978) The chemical and microbiological properties of anaerobic soils and sediments. In *Plant Life in Anaerobic Environments* (D.D. Hook and R.M.M. Crawford, Ed.). Ann Arbor, Michigan: Ann Arbor Science, p. 375–424.

Gardner, W.R. (1960) Dynamic aspects of water availability to plants. *Soil Science*, **89**: 63–73.

Gardner, W.R. and C.F. Ehlig (1962) Some observations on the movement of water to plant roots. *Agronomy Journal*, **54**: 453–456.

Gerwitz, A. and E.R. Page (1974) An empirical mathematical model to describe plant root systems. *Journal of Applied Ecology*, **11**: 773–782.

Ghuman, B.S. and R. Lal (1983) Effect of crop cover on temperature regimes of an Alfisol in the tropics. *Agronomy Journal*, **75**: 931–936.

Grable, A.R. (1966) Soil aeration and plant growth. *Advanced Agronomy*, **18**: 57–106.

Granger, F.J., D.S. Chanasyk, D.H. Male and D.I. Norum (1977) Thermal regime of a prairie snow cover. *Soil Science Society of America Journal*, **41**: 839–842.

Grant, R.F., R.C. Izaurralde and D.S. Chanasyk (1990) Soil temperature under conventional and minimum tillage: Simulation and experimental verification. *Canadian Journal of Soil Science*, **70**: 289–304.

Greacen, E.L. and C.T. Hignett (1976) A water balance model and supply index for wheat in South Australia. CSIRO Australian Division of Soils, Technical Paper no. 27.

Greenwood, D.J., A. Gerwitz, D.A. Stone and A. Barnes (1982) Root development of vegetable crops. *Plant Soil*, **68**: 75–96.

Gregory, P.J., M. McGowan, P.V. Briscoe and B. Hunter (1978) Water relations of winter wheat. I. Growth of the root system. *Journal of Agricultural Science (Cambridge)*, **91**: 91–102.

Groenevelt, P.H. and B.D. Kay (1974) On the interaction of water and heat transport in frozen and unfrozen soils. II: The liquid phase. *Soil Science Society of America Proceedings*, **38**: 400–404.

Gupta, S.C., W.E. Larson and R.R. Allamaras (1984) Predicting soil temperature and soil heat flux under different tillage-surfaces residue conditions. *Soil Science Society of America Journal*, **48**: 223–232.

Guymon, G.L., T.V. Hromadka and R.L. Berg (1980) A one-dimensional frost heave model

based upon simultaneous heat and water flux. *Cold Regions Science and Technology*, **3**: 253–262.

Hamblin, A.P. (1985) The influence of soil structure on water movement, crop root growth and water uptake. *Advances in Agronomy*, **38**: 95–158.

Hanks, R.J., D.D. Austin and W.T. Ondrechen (1971) Soil temperature estimation by a numerical method. *Soil Science Society of America Proceedings*, **35**: 665–667.

Hansen, G.K. (1974) Resistance to water flow in soil and plants, plant water status, stomatal resistance and transpiration of Italian ryegrass, as influenced by transpiration demand and soil water depletion. *Acta Agricultura Scandinavia*, **24**: 83–92.

Harlan, R.L. (1971) Water transport in frozen and partially frozen porous media. *Proceedings, Canadian Hydrology Symposium*, **1**(8): 109–129.

Harris, G.A. (1977) Root phenology as a factor of competition among grass seedlings. *Journal of Range Management*, **30**: 172–177.

Hasfurther, V.R. and R.D. Burman (1974) Soil temperature modeling using air temperature as a driving mechanism. *Transactions, ASAE*, **17**: 78–81.

Heinrichs, D.H. and K.F. Nielsen (1966) Growth responses of alfalfa varieties of diverse genetic origin to different root zone temperatures. *Canadian Journal of Plant Science*, **46**: 291–298.

Hillel, D. (1977) Computer simulation of soil water dynamics. International Development Research Centre, Ottawa, Canada.

Hillel, D. and H. Talpaz (1976) Simulation of root growth and its effect on the pattern of soil water uptake by a nonuniform root system. *Soil Science*, **121**: 307–312.

Hromadka, T.V., G.L. Guymon and R.L. Berg (1981) Some approaches to modeling phase change in freezing soils. *Cold Regions Science and Technology*, 4: 137–145.

Hsiao, T.C. and K.J. Bradford (1983) Physiological consequences of cellular water deficits. In *Limitations to efficient water use in crop production* (H.M. Taylor, W.R. Jordan and T.R. Sinclair, Ed.). American Society of Agronomy, Madison, Wisconsin, p. 227–265.

Huck, M.G. and D. Hillel (1983) A model of root growth and water uptake accounting for photosynthesis, respiration, transpiration and soil hydraulics. In *Advances in Irrigation Research* (D. Hillel, Ed.). New York: Academic Press, vol. II, p. 273–303.

Johnson, I.R. (1983) A model of the partitioning of growth between shoots and roots of vegetative plants. *Annals of Botany*, **55**: 421–431.

Johnson, I.R. and J.H.M. Thornley (1985) Dynamic model of the response of a vegetation grass crop to light, temperature and nitrogen. *Plant Cell Environment*, **8**: 485–499.

Johnson, J. and R.E. Hartman (1919) Influence of soil environment on the root-rot of tobacco. *Journal of Agricultural Research*, **17**: 41–86.

Jones, C.A., W.L. Bland, J.T. Ritchie and J.R. Williams (1991) Simulation of root growth. In *Modeling Plant and Soil Systems* (J. Hanks and J.T. Ritchie, Ed.). American Society of Agronomy, Madison, Wisconsin, Monograph 31, p. 91–123.

Jury, W.A., G. Sposito and R.E. White (1986) A transfer function model of solute transport through soil, I. Fundamental concepts. *Water Resources Research*, **22**: 243–247.

Kaspar, T.C. and W.L. Bland (1992) Soil temperature and root growth. *Soil Science*, **154**: 290–299.

Kay, B.D. and P.H. Groenevelt (1974) On the interaction of water and heat transfer in frozen and unfrozen soils. *Soil Science Society of America Proceedings*, **38**: 395–404.

Klepper, B. (1991) Root-shoot relationship. In *Plant Roots, The Hidden Half* (Y. Waisel, A. Eshel and U. Kafkafi, Ed.). New York, Basel, Hong Kong: Marcel Dekker, Inc., p. 265–286.

Kooistra, M.J., D. Schoonderbeek, F.R. Boone, B.W. Veen and M.J. van Noordwijk (1992) Root-soil contact of maize, as measured by a thin-section technique. II. Effects of soil compaction. *Plant Soil*, **139**: 119–129.

Kramer, P.J. (1988) Changing concepts regarding plant water relations. *Plant Cell Environment*, **11**: 565–568.

Kung, K.J. and T.S. Steenhuis (1986) Heat and moisture transfer in a partly frozen nonheaving soil. *Soil Science Society of America Journal*, **50**: 1114–1122.

Lafolie, F., L. Bruckler and F. Tardieu (1991) Modeling root water potential and soil-root water transport: I. Model presentation. *Soil Science Society of America Journal*, **55**: 1203–1212.

Langholz, H. (1989) A simple model for predicting daily mean soil temperatures. *Journal of Agronomy and Crop Science*, **163**: 312–318.

Lascano, R.J. and C.H.M. van Bavel (1984) Root water uptake and soil water distribution: Test of an availability concept. *Soil Science Society of America Journal*, **48**: 233–237.

Legget, R.F. and C.B. Crawford (1952) Soil temperatures in waterworks practice. *Journal of the American Waterworks Association*, **44**: 923–939.

Lockhart, J.A. (1965) Cell extension. In *Plant Biochemistry* (J. Bonner and J.E. Varner, Ed.). New York: Academic Press, p. 826–829.

Lungley, D.R. (1973) The growth of root systems - A numerical computer simulation model. *Plant Soil,* **38**: 145–149.

Luxmoore, R.J., L.H. Stolzy and J. Letey (1970) Oxygen diffusion in the soil-plant system. I. A model. *Agronomy Journal,* **62**: 317–322.

MacKey, J. (1973) The wheat root. In *Proceedings, 4th International Wheat Genetics Symposium.* Missouri Agricultural Experiment Station, Columbia, p. 827–842.

May, L.H., F.H. Chapman and D. Aspinall (1965) Quantitative studies of root development. I. The influence of nutrient concentration. *Australian Journal of Biological Science,* **18**: 25–35.

McMichael, B.L., J.J. Burke, T.D. Berlin, J.L. Hatfield and J.E. Quisenberry (1985) Root vascular bundle arrangements among cotton strains and cultivars. *Environmental and Experimental Botany,* **25**: 23–30.

Meikle, R.W. and T.R. Treadway (1979) A mathematical method for estimating soil temperatures. *Soil Science,* **28**: 226–242.

Mengel, B.D. and S.A. Barber (1974) Development and distribution of the corn root system under field conditions. *Agronomy Journal,* **66**: 341–344.

Meyer, V.S. and J.T. Ritchie (1980) Resistance to water flow in the sorghum plant. *Plant Physiology,* **65**: 33–39.

Miller, R.D. (1973) Soil freezing in relation to pore water pressure and temperature. In *Permafrost: The North American Contribution to the 2nd International Conference on Permafrost, Yakutsk, 13–28 July.* Washington, D.C.: National Academy of Sciences, p. 344–352.

Miller, R.D. (1977) Lens initiation in secondary heaving. In *Proceedings, International Symposium on Frost Action in Soils, Luleå, Sweden, 16–18 February,* vol. 2, p. 68.

Miller, R.D. (1978) Frost heaving in non-colloidal soils. *Proceedings, 3rd International Conference on Permafrost, 10–13 July. Edmonton, Alberta.* Ottawa: National Research Council of Canada, vol. 1, p. 707–713.

Miller, R.D., J.P.G. Loch and E. Bresler (1975) Transport of water and heat in a frozen permeameter. *Soil Science Society of America Proceedings,* **39**: 1029–1036.

Miller, P.C., M.P. Miller, M. Blake-Jacobson, F.S. Chapin III, K.R. Everett, D.W. Hilbert, J. Kummerow, A.E. Linkins, G.M. Marion, W.C. Oechel, S.W. Roberts and L. Stuart (1984) Plant-soil processes in *Eriophorum vaginatum* tussock tundra in Alaska: A systems modeling approach. *Ecological Monographs,* p. 361–405.

Mozafar, A. and J.J. Oertli (1992) Root-zone temperature and salinity: Interacting effects on tillering, growth and element concentration in barley. *Plant and Soil,* **139**: 31–38.

Musick, J.T., L.L. New and D.A. Dusek (1976) Soil water depletion – Yield relationships of irrigated sorghum, wheat and soybeans. *Transactions, ASAE,* **19**: 489–493.

Neild, R.E. (1971) Growing season air-soil temperature relationship at Lincoln, Nebraska. Nebraska Agricultural Experiment Station Research Bulletin, p. 242.

Nielsen, K.L., J.P. Lynch, A.G. Jablokow and P.S. Curtis (1994) Carbon cost of root systems: An architectural approach. *Plant Soil,* **165**: 262–269.

Nielson, K.F. and E.C. Humphries (1966) Effects of root temperature on plant growth. *Soils Fertilization,* **29**: 1–7.

Nimah, M.N. and R.J. Hanks (1973) Models for estimating soil water, plant and atmospheric interrelations. I. Description and sensitivity. *Soil Science Society of America Proceedings,* **37**: 522–527.

Nnyamah, J.U. (1977) Root water uptake in a Douglas fir frost. Ph.D. Thesis, University of British Columbia, Vancouver, p. 154.

Nye, P.H. (1966) The effect of the nutrient intensity and buffering power of a soil and the absorbing power, size and root hairs of a root, on nutrient absorption by diffusion. *Plant Soil,* **25**: 81–105.

Nye, P.H. and F.H.C. Marriott (1969) A theoretical study of the distribution of substances around roots resulting from simultaneous diffusion and mass flow. *Plant Soil,* **30**: 459–472.

Nye, P.H. and P.B.H. Tinker (1969) The concept of a root demand coefficient. *Journal of Applied Ecology,* **6**: 293–300.

Nye, P.H., J.L. Brewster and K.K.S. Bhat (1975) The possibility of predicting solute uptake and plant growth response from independently measured soil and plant characteristics. I. Theoretical basis of the experiments. *Plant Soil,* **42**: 161–170.

Oates, K. and S.A. Barber (1987) Nutrient uptake: A microcomputer program to predict nutrient absorption from soil by roots. *Journal of Agronomy Education,* **16**: 65–68.

O'Neill, K. and R.D. Miller (1982) Numerical solutions for a rigid ice model of secondary frost heave. USA Cold Regions Research and Engineering Laboratory, CRREL Report 82–13.

Parton, W.J. (1984) Predicting soil temperatures in the shortgrass steppe. *Soil Science,* **138**: 93–101.

Péwé, T.L. (1983) Alpine permafrost in the contiguous United States: A review. *Arctic and Alpine Research,* **5**: 145–156.

Ponnamperuma, F.N. (1984) Effects of flooding on soils. In *Flooding and Plant Growth* (T.T. Kozlowski, Ed.). Orlando, Florida: Academic Press, p. 9–45.

Porter, J.R., B. Klepper and R.K. Belford (1986) A model (WHTROOT) which synchronizes root growth and development with shoot development for winter wheat. *Plant Soil*, **92**: 133–145.

Reicosky, D.C. and J.T. Ritchie (1976) Relative importance of soil resistance and plant resistance in root water absorption. *Soil Science Society of America Journal*, **40**: 293–297.

Rendig, V.V. and H.M. Taylor (1989) *Principles of Soil–Plant Interrelationships*. New York: McGraw-Hill Publishing Co., p. 275.

Reynolds, J.F. and J.H. Thornley (1982) A shoot-root partitioning model. *Annals of Botany*, **49**: 585–597.

Reynolds, J.F. and P.W. Leadley (1992) Modeling the response of arctic plants to changing climate. In *Arctic Ecosystem in a Changing Climate, An Ecological Perspective* (F.S. Chapman III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda, Ed.). New York: Academic Press, p. 413–438.

Richards, L.A. (1931) Capillary conduction of liquid through porous media. *Physics*, **1**: 318–333.

Richtmeyer, R.D. and K.W. Morton (1967) *Different Methods for Initial-Value Problems*. New York, Interscience Publishers, 2nd edition, p. 405.

Rijtema, P.E. (1965) An analysis of actual evapotranspiration. Agricultural Research Report 659. Pudoc, Wageningen, p. 107.

Roberts, J.K.M., J. Callis, O. Jardetsky, V. Walbot and M. Freeling (1984a) Mechanism of cytoplasmic pH regulation in hypoxic maize root tips and its role in survival under hypoxia. *Proceedings, National Academy of Sciences, USA*, **81**: 3379–3383.

Roberts, J.K.M., J. Callis, O. Jardetsky, V. Walbot and M. Freeling (1984b) Cytoplasmic acidosis as a determinant of flooding intolerance in plants. *Proceedings, National Academy of Sciences, USA*, **81**: 6029–6033.

Rosema, A. (1975) Simulation of the thermal behavior of bare soils for remote sensing purposes. In *Heat and Mass Transfer in the Biosphere. Part I. Transfer Processes in the Plant Environment* (D.A. De Vries and N.H. Afgan, Ed.). New York: John Wiley and Sons, Inc., p. 109–123.

Russell, R.S. (1977) The growth and form of root systems. In *Plant Root Systems: Their Functions and Interaction with the Soil* (R.S. Russel, Ed.). London: McGraw-Hill Book Company, p. 30–61.

Russell, R.S. and M.J. Goss (1974) Physical aspects of soil fertility—The response of roots to mechanical impedance. *Netherlands Journal of Agricultural Science*, **22**: 305–318.

Shul'gin, A.M. (1967) Soil climate and its control. National Technical Information Service, U.S. Department of Commerce, Springfield, Virginia, Translation TT-72-51048 (translated from Russian).

Simmons, C.S. (1982) A stochastic-convective transport representation of dispersion in one-dimensional porous media systems. *Water Resources Research*, **18**: 1193–1214.

Skiles, J.W., J.D. Hanson and W.J. Parton (1982) Simulation of above and below ground carbon and nitrogen dynamics of *Bouteloua gracilis* and *Agropyron smithii*. In *Analysis of Ecological Systems: State of the Art in Ecological Modelling* (W.K. Lavenroth, G.V. Skogerboe and M. Flug, Ed.). Amsterdam: Elsevier.

Smucker, A.J.M. and R.M. Aiken (1992) Dynamic root responses to water deficits. *Soil Science*, **154**: 281–289.

Stem, K.R. (1982) *Introductory Plant Biology*. Dubuque, Iowa: Wm. C. Brown Company Publishers, p. 493.

Stone, J.A. and H.M. Taylor (1983) Temperature and the development of the taproot and lateral roots of four indeterminate soybean cultivars. *Agronomy Journal*, **75**: 613–618.

Stone, J.A., T.C. Kaspar and H.M. Taylor (1983) Predicting soybean rooting depth as a function of soil temperature. *Agronomy Journal*, **75**: 1050–1054.

Taylor, H.M. (1983) Managing root systems for efficient water use: An overview. In: *Limitations to Efficient Water Use in Crop Production* (H.M. Taylor, W.R. Jordan and T.R. Sinclair, Ed.). American Society of Agronomy, Madison, Wisconsin, p. 87–111.

Taylor, H.M. and L.F. Ratliff (1969) Root elongation rates of cotton and peanuts as a function of soil strength and soil water content. *Soil Science*, **108**: 113–119.

Taylor, H.M. and B. Klepper (1971) Water uptake by cotton roots during an irrigation cycle. *Austrialian Journal of Biological Science*, **24**: 853–859.

Taylor, H.M. and B. Klepper (1973) Rooting density and water extraction patterns for corn (*Zea mays* L.). *Agronomy Journal*, **65**: 965–968.

Taylor, H.M. and B. Klepper (1975) Water uptake by cotton root systems: An examination of assumptions in the single root model. *Soil Science*, **120**: 57–67.

Taylor, G.S. and J.N. Luthin (1978) A model for coupled heat and moisture transfer during soil freezing. *Canadian Geotechnical Journal*, **15**: 548–555.

Taylor, H.M. and G.F. Arkin (1981) Root zone modification: Fundamentals and alternatives. In *Modifying the Root Environment to Reduce Crop Stress* (G.F. Arkin and H.M. Taylor, Ed.). American Society of Agricultural Engineers, St. Joseph, Missouri, ASAE Monograph, p. 3–17.

Taylor, H.M. and G.S. Brar (1991) Effect of soil compaction on root development. *Soil and Tillage Research*, 19: 111–119.

Tennant, D. (1976) Root growth of wheat. I. Early pattern of multiplication and extension of wheat roots including effects of levels of nitrogen, phosphorus and potassium. *Australian Journal of Agricultural Research*, 27: 183–196.

Tillotson, W.R. and R.J. Wagenet (1982) Simulation of fertilizer under cropped situations. *Soil Science*, 133: 133–143.

Van Bavel, C.H.M. and D.I. Hillel (1976) Calculating potential and actual evapotranspiration from a bare soil surface by simulation of concurrent flow of water and heat. *Agricultural Meteorology*, 17: 453–476.

Van den Honert, T.H. (1948) Water transport in plants as a catenary process. Discussion. *Faraday Chemical Society*, 3: 146–153.

van Noordwijk, M.J., J. Kooistra, F.R. Boone, B.W. Veen and D. Schoonderbeek (1992) Root-soil contact of maize as measured by a thin-section technique. I. Validity of the method. *Plant Soil*, 139: 109–118.

Vauclin, M., S.R. Vieira, R. Bernard and J.L. Hatfield (1982) Spatial variability of surface temperature along two transacts of bare soil. *Water Resources Research*, 6: 1677–1686.

Voorhees, W.B., R.R. Allmaras and C.E. Johnson (1981) Alleviating temperature stress. In: *Modifying the Root Environment to Reduce Crop Stress* (G.F. Arkin and H.M. Taylor, Ed.). American Society of Agricultural Engineers, St. Joseph, Missouri, ASAE Monograph, p. 217–266.

Vos, J. and J. Groenwold (1986) Root growth of potato crops on a marine-clay soil. *Plant Soil*, 94: 17–33.

Welbank, P.J., M.J. Gibb, P.J. Taylor and E.D. Williams (1974) Root growth of cereal crops. Rothamsted Experimental Station Report for 1973, Part 2, p. 26–66.

Wierenga, P.J. and C.T. DeWit (1970) Simulation of heat flow in soils. *Soil Science Society of America Proceeding*, 34: 845–848.

Willatt, S.T. and H.M. Taylor (1978) Water uptake of soybean roots as affected by their depth and soil water content. *Journal of Agricultural Science*, 90: 205–213.

Willatt, S.T. and K.A. Olsson (1982) Root distribution and root uptake by irrigated soybeans on a duplex soil. *Australian Journal of Soil Research*, 20: 139–146.

Yang, S.J. and E. de Jong (1971) Effect of soil water potential and bulk density on water uptake patterns and resistance to flow of water in wheat plants. *Canadian Journal of Soil Science*, 51: 211–220.

Yang, S.J. and E. de Jong (1972) Effect of aerial environment and soil water potential on the transpiration and energy status of water in wheat plants. *Agronomy Journal*, 61: 571–578.

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13. ABSTRACT *(Maximum 200 words)*

Understanding the growth and function of plant roots in cold climates is critical, but examination of root systems to elucidate their link to production is expensive and labor-intensive. Limited information is available on the root growth and functions of plants grown in northern climates. Our objective is to present an overview of the influence of physical edaphic factors on plant root systems with special emphasis on models that are available for simulating root growth. This report summarizes the impact of the soil physical environment (soil water, soil temperature, soil air, physical impedance, and spatial variability) on root uptake and growth. Roots grow because new cells are formed in the meristematic tissue near the root tip, and these newly formed cells increase in volume, pushing the root tip forward if growth conditions are satisfactory. Rapid elongation of primary roots, combined with well-developed secondary roots, allows the plants to exploit moisture and nutrients from a greater soil volume. Root and shoots are strongly interdependent. The roots receive photosynthates and growth hormones from shoots and in return furnish water and nutrients to the shoots. Several root growth models have been developed during the past decade; however, none addresses the problems associated with cold regions. The models reported in the literature can be classified as 1) simple models, 2) carbon partition models, 3) growing degree day-based models, 4) soil parameter-based models, and 5) arctic plant growth models.

14. SUBJECT TERMS

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